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Observations on the Genus *Santalum* (Santalaceae) in Hawai'i[1]

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ABSTRACT: Some of the taxonomic problems of species of *Santalum* in Hawai'i are resolved by proposing one new taxon and two combinations. These are based on observations of the genus in the field, herbarium studies, and anatomical differences found.

THE HAWAIIAN SANDALWOODS are of interest to those concerned with both the natural history and socioeconomic history of Hawai'i. The taxonomy of the genus *Santalum* has been studied by several individuals, and yet there are still problems within the genus. Most of the recent reviewers have considered two main groups of the genus in Hawai'i. These groups can be distinguished by the shape of the perigonal tube and characteristics of the drupe (Rock 1916, Skottsberg 1927, 1930*b*, Tuyama 1939, Fosberg 1948). In one—the *freycinetianum* group, which previous authors have considered to include *S. freycinetianum* Gaud., *S. pyrularium* Gray, *S. lanaiense* (Rock) Rock, and *S. haleakalae* Hbd.—the perigonal tube is campanulate to cylindrical and it is longer than its widest diameter. Skottsberg (1930*a*) has suggested that this group is ornithophilous, based on the length of the tube, the red color, and the quantity of nectar, but I have not often seen birds feeding on the flowers of *Santalum*. The perigonal ring is a conspicuous subapical scar on the drupe, surrounding the broad, conical tip of the ovary. The flowers of these taxa are often red, at least when exposed to sunlight, though some plants from Kaua'i tend to have green flowers under most circumstances.

In the second—the *ellipticum* group, which has been considered to include *Santalum ellipticum* Gaud., *S. paniculatum* H. & A., and *S. pilgeri* Rock—the perigonal tube is obconical to funnel-shaped and it is not much longer than its widest diameter. The perigynous ring is positioned more apically than in the *freycinetianum* group, and when the ovary is prolonged beyond that scar, it is acuminate. However, the distinction made by previous authors concerning the position of the perigynous ring on the drupe is not as clearly marked as they have indicated. The difference is only a matter of degree, and it is not possible to use this character alone to segregate plants into two groups. It is interesting that Skottsberg (1927) and Degener (1940*a*) are in decided disagreement as to which of the two groups has the semi-inferior ovary with the subapical perigynous ring and which has the inferior ovary with the apical perigynous ring.

The flowers of the *ellipticum* group are usually greenish at anthesis, and never a burgundy red, though older exposed flowers of most taxa may be brownish yellow, or rarely salmon-to-red colored on the inner lobes of the flower and in the floral tube.

The study of the comparative anatomy of the genus in Hawai'i has taken me to numerous populations in the field, and, having considered the variation of the Hawaiian taxa, it seems appropriate to present my observations on each species within each group. Following is a modification of the keys of previous authors to the taxa as I recognize

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TABLE 1

GROSS MORPHOLOGY OF THE HAWAIIAN TAXA OF *Santalum*

SPECIES	FLOWER LENGTH (mm)	PEDICEL LENGTH (mm)	FRUIT LENGTH (mm)	LEAF LENGTH (mm)	LEAF WIDTH (mm)	PETIOLE LENGTH (mm)
S. ellipticum	4– 7	0–1	9–12	25– 61	17–40	2–15
S. ellipticum var. *littorale*	4– 7	0–1	8–15	25– 55	20–40	2–12
S. paniculatum	5– 7	0–1	8–12	25– 60	20–35	2–10
S. paniculatum var. *pilgeri*	4– 8	0–1	10–12	55– 80	25–45	4–15
S. haleakalae	8–17	2–4	10–15	25– 75	20–60	2– 7
S. freycinetianum	6–13	2–3	8–15	45–120	13–44	7–25
S. freycinetianum var. *pyrularium*	7–17	2–6	8–24	40–115	18–40	5–18
S. freycinetianum var. *lanaiense*	9–16	2–4	11–15	40– 85*	20–75*	4–18
S. freycinetianum var. *auwahiense*	8–16	1–4	12–17	60– 90	20–40	10–18

*Largest measurements were from the holotype.

TABLE 2

INSULAR DISTRIBUTION OF THE TAXA OF *Santalum* IN THE HAWAIIAN ISLANDS

SPECIES	Laysan	Kaua'i	O'ahu	Moloka'i	Lāna'i	Maui	Kaho'olawe	Hawai'i
Freycinetianum group								
S. freycinetianum								
var. *freycinetianum*			×	×				
var. *pyrularium*		×						
var. *lanaiense*					×			
var. *auwahiense*						×		
S. haleakalae						×		
Ellipticum group								
S. ellipticum								
var. *ellipticum*		×	×	×	×	×	×*	×
var. *littorale*	×†		×					
S. paniculatum								
var. *paniculatum*								×
var. *pilgeri*								×

*Presumably extinct.
†Extinct.

them, as well as a table (Table 1) of characters for the species in Hawai'i. A list of synonyms and usages is included in the discussion for each taxon. Table 2 shows the distribution of the taxa in the Hawaiian Islands.

The intention of this paper is not to remonograph the Hawaiian species of *Santalum*, but rather to evaluate the work of previous authors in the light of more recent evidence (Stemmermann 1980). For this reason specimens are cited only where coverage by previous authors is considered inadequate.

KEY TO THE HAWAIIAN SPECIES OF THE GENUS *Santalum*

1. Flowers with campanulate to cylindrical perigonal tubes, the length of the tube greater than its widest diameter, at least the older flowers reddish either internally or externally, or if not reddish then greater than 10 mm in length exclusive of the pedicel, flowers not very aromatic; drupe with subapical perigynous scar, the often broad conical tip of the

ovary sometimes prolonged beyond the scar; leaves with abaxial stomata only (*freycinetianum* group).

2. Inflorescence terminal, very dense and congested, the peduncles of dichasia obscured, bracts up to 5 mm long conspicuous in inflorescences in bud, often persistent to anthesis; flowers deep red on outside of lobes, inner surfaces of floral tube white turning deep red with age; leaves sessile to subsessile, petiole 2–7 mm long, blades ovate, obovate, or orbicular, coriaceous, often purplish olive green; adaxial epidermal cells bottle-shaped in leaf cross section, abaxial leaf surface pale. (east Maui)
   5. *S. haleakalae*
2. Inflorescence axillary, or if terminal, neither very dense nor congested, bracts 1–4 (rarely 5) mm long, not conspicuous in inflorescence of buds, caducous; flowers deep red, or greenish yellow on outside of lobes, inner surface white or yellowish, usually turning deep red with age; leaves subsessile to petiolate, petiole 4–25 mm long, blades orbicular to elliptic, chartaceous to coriaceous, not purplish, but various shades of green, adaxial epidermal cells not bottle-shaped in leaf cross section.
   3. Leaves chartaceous, narrowly elliptic to narrowly ovate, apices acute, occasionally rounded, abaxial leaf surface usually not much paler than upper leaf surface, flowers yellowish or reddish in bud.
      4. Floral tube campanulate, or if cylindrical, not slightly constricted at the throat; disk lobes clavate, leaves conduplicate-falcate. (O'ahu, Moloka'i)
         1. *S. freycinetianum* var. *freycinetianum*
      4. Floral tube cylindric, sometimes slightly constricted at the throat; disk lobes lingulate, leaves plane, or infrequently conduplicate. (Kaua'i)
         4. *S. freycinetianum* var. *pyrularium*
   3. Leaves chartaceous to coriaceous, ovate to orbicular, or elliptic, apices rounded to obtuse (rarely acute), abaxial leaf surfaces usually paler than adaxial leaf surfaces, flowers red in bud.
      5. Leaves ovate to elliptic, yellowish green, petioles 10–18 mm long; flowers in axillary panicles. (Maui)
         2. *S. freycinetianum* var. *auwahiense*
      5. Leaves orbicular to ovate, dark green or olive green, petioles 4–18 mm long; flowers in terminal inflorescence. (Lāna'i)
         3. *S. freycinetianum* var. *lanaiense*

1. Flowers with campanulate to conical perigonal tubes, the length of the tube about equal to its widest diameter, usually greenish in bud and in flower, becoming tinged with brown, orange, or rarely salmon on the inside of the perigonal tube in age, but seldom deep red, generally sweetly aromatic; drupe with apical perigynous scar with only a thin acuminate tip of the ovary prolonged beyond the scar; leaves with adaxial and abaxial stomata, or only abaxial stomata (*ellipticum* group).
   6. Leaves ovate, obovate, elliptic or orbicular, dull gray-green when fresh (sometimes obscured in herbarium material), both surfaces generally the same color, coriaceous or succulent, stomata on abaxial and adaxial leaf surfaces; shrubs to small trees.
      7. Leaves coriaceous, but not succulent, the older leaves rarely greater than 1.0 mm thick, multiple epidermis and compound hypodermis absent; fruit without bloom or only slightly glaucous; shrubs to small trees. (Kaua'i, O'ahu, Moloka'i, Lāna'i, Maui, Kaho'olawe, Hawai'i)
         6. *S. ellipticum* var. *ellipticum*
      7. Leaves succulent, the older leaves to 2.0 mm thick, multiple epidermis and multicellular hypodermis often present on both leaf surfaces; fruit very glaucous; shrubs less than 1 m. (O'ahu, Laysan)
         7. *S. ellipticum* var. *littorale*
   6. Leaves ovate, obovate, or elliptic, blue-green, golden-green, or orange-green, lower

surface often paler than upper surface, or leaves chartaceous, stomata evenly distributed on lower surface only (very rare in adaxial epidermis).

8. Leaves ovate to obovate, coriaceous, orange or blue-green above, conspicuously paler below, shrubs or trees. (Hawai'i)

8. *S. paniculatum* var. *paniculatum*

8. Leaves elliptic to ovate, chartaceous, often convexly curved, not conspicuously paler below, trees. (Hawai'i)

9. *S. paniculatum* var. *pilgeri*

DISCUSSION

Freycinetianum group

1. *Santalum freycinetianum* Gaudichaud 1830, Voyage autour du monde . . . , Botanique, p. 442, tab. 45. Type: Gaudichaud (P), *insulis Sandwicensibus* (Wahou), alt. 350–400 hex. [Gaudichaud's altitudes were recorded in fathoms (St. John 1977, personal communication)]; De Candolle (1875), Rock (1916), Skottsberg (1926, 1927), Degener (1937*b*, 1940*a*), St. John (1947), Stauffer [1964, annotations in herbaria (BISH, HAW)], St. John (1973).
   S. pyrularium (*pro parte non* Gray) Wawra 1875.
   S. longifolium Meurisse 1892.
   S. freycinetianum Gaud. var. *longifolium* (Meurisse); Degener (1937*b*), St. John (1973).
   S. freycinetianum Gaud. var. *ellipticum* (*auct. non* Gaud.) Mann 1866; Gray (ms), Hillebrand (1888).
   S. ellipticum (*auct. non* Gaud.) Gray 1860; Rock (1913).

Santalum freycinetianum is the common sandalwood found in dry to mesic forests on O'ahu, and has been considered to be confined to that island. Once Rock (1916) clarified the nomenclature problems with this species, he and subsequent authors (Skottsberg 1927, Degener 1937*b*) described it adequately. The flower and leaf lengths are variable, as is the general appearance of the plants. They may range from low shrubs, sometimes less than 1 m tall, found in xeric sites, to trees up to 13 m in height with a diameter breast height (dbh) of greater than 50 cm. [St. John (1947) recorded one at 70 cm diameter.] The leaves are often conduplicate-falcate and frequently appear wilted. The petioles are 10–25 mm long. The new leaves, petioles, and midribs are usually red. Previous authors have considered this species as being confined to O'ahu, though both Skottsberg (1944) and Stauffer (who was reviewing the family on a worldwide basis but died prior to publishing his views on the Hawaiian taxa) suggested that *S. pyrularium* from Kaua'i might be included in *S. freycinetianum* (annotations on herbarium specimens at BISH and HAW, 1964). Rock (1916) noted that some plants from Maui also resembled this taxon.

In my own collections from Moloka'i and in specimens from the herbaria at the Bishop Museum and the University of Hawaii, a sandalwood of the *freycinetianum* group is represented, although no such plants have previously been recorded from that island. The population shown to me by forest ranger J. Lindsey at an elevation of 3250 ft on a fairly steep slope on Makakupa'ia Ridge in scrubby vegetation of *Dicranopteris*, *Metrosideros*, *Styphelia*, *Dodonaea*, and *Dubautia* resembles scrubby forms of *S. freycinetianum* found in similar habitats on O'ahu. Other minor components of the vegetation in the vicinity include *Lysmachia*, *Exocarpos*, and *Scaevola gaudichaudii*. In his introduction to the genus *Santalum*, Degener (1940*a*) states that his no. 5308 was an undescribed species of sandalwood he had collected in sterile condition south of Kaulahuki, Moloka'i. Though I have not been able to locate Degener's collection, I feel that this may represent this same taxon. Recently, I and other botanists working on the U.S. Fish and Wildlife Service Hawaiian Forest Bird Survey located several more populations on Moloka'i, including a collection

from near Kaulahuki. Other collections from Moloka'i of this same taxon: HAW: *L. E. Bishop* 1733, collected from 3500 ft in the woods south of Waikolu Valley Lookout; *L. E. Bishop* 1746 from the west ridge of Ōhi'a Gulch, elev. 2100 ft; *R. Hobdy s.n.* collected from forestry boundary overlooking Hālawa Valley. BISH: *Degener* 5306 (sterile, but probably of this taxon), collected from east Ōhi'a Ridge. USFWS uncataloged plants from Moloka'i to be distributed at a later date: *Stemmermann & Montgomery* 3896, elev. 2840 ft, ridge east of Kua Gulch, Kamalo; *Warshauer & McEldowney* 2332, elev. 3750 ft, Kawela Ridge.

The Moloka'i plants range from shrubs with narrow acute leaves found on rather dry slopes in open-canopied vegetation, to trees with broadly ovate leaves with acute to obtuse apices found in mesic forests. The leaves are plane, or conduplicate-falcate with petioles 10–20 mm long, and, as with *Santalum freycinetianum* from O'ahu, may appear wilted. Though Degener (1940*a*) suggests that the plant he collected is a new species, in comparing the Moloka'i specimens encountered in the field and herbaria with *S. freycinetianum*, the Moloka'i plants fall into the range of variation recorded for *S. freycinetianum*, except for the specimen collected by Hobdy. Hobdy's collection more closely resembles some of the low-elevation plants from Maui in that its broad leaves have rounded to obtuse apices. Even with this range of variability, all the red-flowered plants from Moloka'i can be referred to as *S. freycinetianum sensu stricto*, although the taxon from Moloka'i is probably intermediate between the typical *S. freycinetianum* from O'ahu and *S. freycinetianum* var. *auwahiense* from low elevations on Maui. With further collections of plants from Moloka'i it may be possible to recognize the Moloka'i plants as distinct from *S. freycinetianum* at the varietal level, but that should only be done when the range of variation is better understood.

It is interesting to note the sandalwood pit on the road to the Waikolu Lookout. It has been recorded that in many instances a hole was dug the length, depth, and breadth of a ship, and then filled with sandalwood (Rock 1916, 1917, St. John 1947). This quantity of sandalwood would then be traded for a ship. Several such pits are known throughout the archipelago, but the location of this pit is problematic in that no collections of treelike sandalwoods from this area have been reported by Hillebrand (1888), Rock (1913, 1916), Skottsberg (1927), or St. John (1947, 1973), and only a few have been noted in the present study. Either the harvest of sandalwood had a more severe impact on Moloka'i than elsewhere, or a subsequent decline may account for the present scarcity of *Santalum* in the vicinity. Yet another possibility is that these pits served some other function than previously suggested.

2. ***Santalum freycinetianum* Gaud. var. *auwahiense*** var. nov.

Figure 1

S. haleakalae Hbd. *sensu* Rock 1913 as to the lowland Auwahi specimens; Stauffer [1964, annotations in herbaria (BISH, HAW)].

The populations of long-leaved sandalwoods found on east and west Maui below approximately 5000 ft elevation closely resemble some *Santalum freycinetianum* found in the mesic forests on O'ahu. Above approximately 5000 ft on east Maui there is a gradation to typical *S. haleakalae*, but affinities of the lower-elevation plants with typical *S. freycinetianum* are apparent. Differences in leaf and petiole length separate *S. haleakalae* from the low-elevation plants. The leaves of *S. haleakalae* are stiff and coriaceous, and dark purplish olive green, while the lowland plants have chartaceous light-green leaves. The unique urn-shaped upper epidermal cells observed in *S. haleakalae* (Stemmermann 1980) are also lacking in the low-elevation plants.

While Rock (1916) included plants from Auwahi in his conspectus of *Santalum haleakalae*, he stated that these plants are closely allied with *S. freycinetianum*, which he then called *S. ellipticum*. These plants differ from *S. freycinetianum* in that their

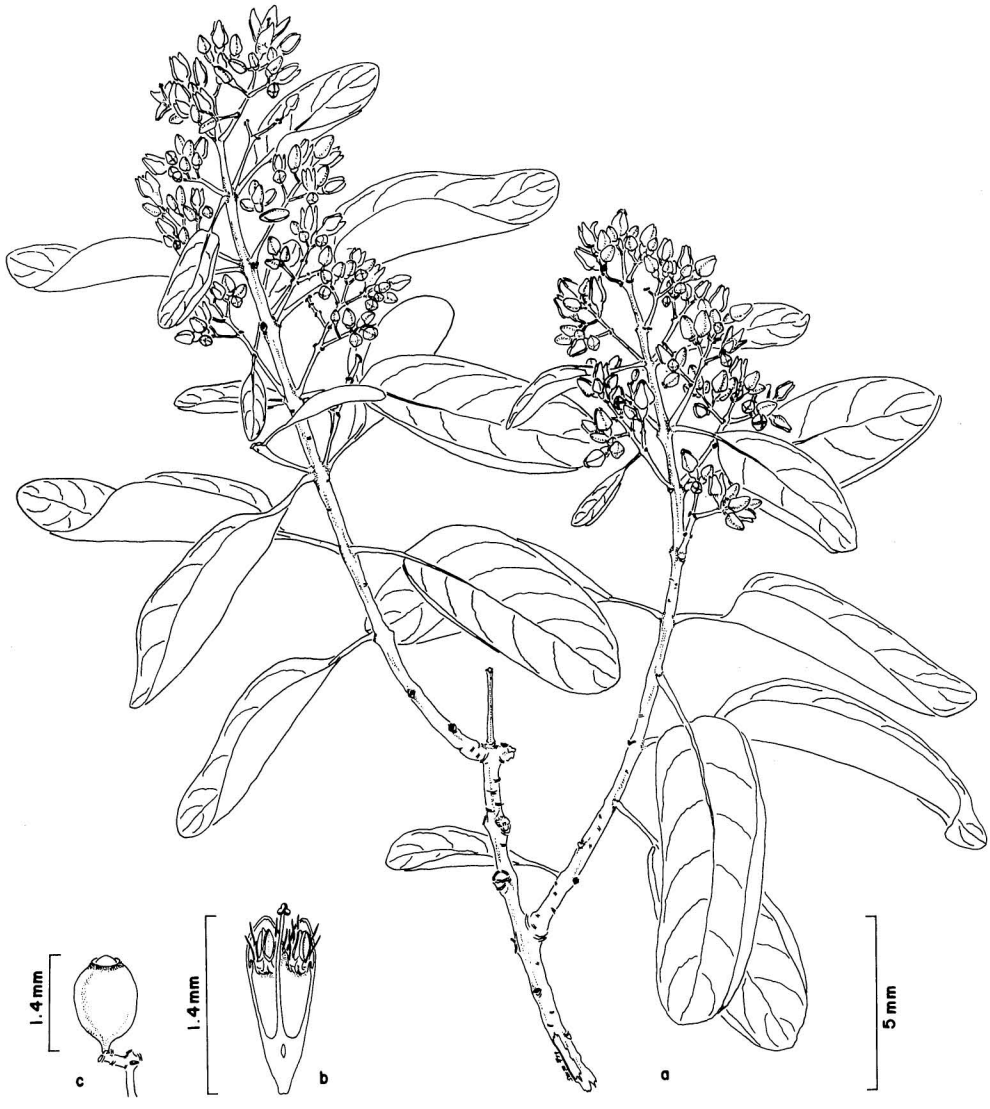

FIGURE 1. *Santalum freycinetianum* Gaud. var. *auwahiense* Stemmermann, from holotype. *a*, branch; *b*, flower; *c*, fruit.

leaves are more coriaceous than typical *S. freycinetianum* from O'ahu, usually with rounded to obtuse apices as opposed to acute in typical *S. freycinetianum*. As in *S. freycinetianum* from O'ahu, the leaves may be conduplicate-falcate, and their undersides pale (not normally considered a character of *S. freycinetianum*, but apparent in several herbarium collections of that taxon). Their flowers are burgundy, and sometimes longer (8–16 mm) than those of *S. freycinetianum* (6–13 mm). The inflorescence is congested to lax in the lowland Maui plants and axillary, but not as congested as in *S. haleakalae*, where the flower mass obscures the axis of the inflorescence. Nor is it as lax as in *S. freycinetianum*, although even with *S. freycinetianum* a few individuals can be seen with rather tight inflorescences. The lowland plants have axillary inflorescences, while the inflorescence of *S. haleakalae* is terminal.

Despite their differences from *Santalum freycinetianum* and their intergradation with *S. haleakalae*, the affinities of these plants with *S. freycinetianum* should be emphasized. The presence of these plants on west Maui, as well as east Maui, suggests that at one time such plants may have occurred throughout the lowlands of Maui, but habitat depletion (and perhaps the effects of sandalwood trade) in such areas has been extensive, and the plants exist now only in relict pockets. On east Maui, such populations intergrade with *S. haleakalae*, another taxon of the *freycinetianum* group that is adapted to the subalpine ecosystem.

The lowland Maui plants have been shown to resemble *Santalum freycinetianum*, and if probable evolutionary trends in the Hawaiian archipelago are considered, it is reasonable to conclude that these plants are more likely derived from an ancestral type similar to *S. freycinetianum* than an ancestral type similar to the alpine-adapted *S. haleakalae*. Furthermore, these plants probably gave rise to *S. haleakalae*. With this consideration I propose that the plants of lowland Maui be referred to as *S. freycinetianum* Gaud. var. ***auwahiense*** var. nov.

DIAGNOSIS: Folia chartacea vel coriacea, apicibus rotundis vel obtusis; foliorum paginae abaxiales pallidiorae quam paginae adaxiales.

Leaves chartaceous to coriaceous, apices rounded to obtuse; abaxial leaf surface paler than adaxial surface.

HOLOTYPE: Auwahi Forest Reserve, 4000 ft elev. *L. Stemmermann & J. Kjargaard* 2149 (BISH). Isotypes are to be distributed.

Other collections: BISH: *C. N. Forbes* 2364. M., ridge in upper part of Olowalu Valley; *J. Rock* 8659, Kaluikuinui, Auwahi; *J. Rock* 27,002, Auwahi; *H. U. Stauffer & G. W. Gillett* 5892, 1200 m, Auwahi. HAW: *D. Herbst, C. H. Lamoureux, & E. Bishop* 728, 4000 ft, Auwahi; *E. Bishop, W. Gagné, & S. Montgomery* 047161, Manawainui Gulch, west Maui; *L. Stemmermann & R. Hobdy* 746, 4000 ft, Auwahi; *L. Stemmermann & R. Hobdy* 757, 4000 ft, Auwahi; *L. Stemmermann & R. Hobdy* 758, 3900 ft, Auwahi; *R. Hobdy & W. Wong* s.n. 17 January 1973, Helu Peak between Kaua'ula and Launiupoko Streams.

DISCUSSION: This variety differs from the related *Santalum freycinetianum* var. *freycinetianum*, which has chartaceous leaves with acute apices. Furthermore, the abaxial leaf surface in the typical variety is usually not much paler than the upper surface. The other closely related taxon, *S. haleakalae*, has ovate subsessile leaves and a very dense congested inflorescence while *S. freycinetianum* var. *auwahiense* has elliptic petiolate leaves with an axillary inflorescence (Figure 1).

The epithet is derived from the island of Maui, and the neuter Latin adjectival suffix *-ense*.

3. *Santalum freycinetianum* Gaud. var. *lanaiense* Rock 1913, Indigenous trees of Hawaii, privately published, Honolulu. Type: *Rock* 10,061 (BISH), Lāna'i on spur of the main ridge, Lāna'ihale, elev. about 3000 ft.

   S. lanaiense Rock 1916; Skottsberg (1927), Degener (1940*a*), St. John (1973).

   S. haleakalae Stauffer 1964, annotations in herbaria (BISH, HAW).

Santalum freycinetianum var. *lanaiense* is a variable taxon found only on Lāna'i, and is the only taxon of the *freycinetianum* group reported from that island. Although he had not seen it in the field, Skottsberg (1927) described it as an excellent species that could not be confounded with any other. However, on the basis of my studies, it is now recommended that this taxon is best recognized at the varietal level. On some specimens the leaves are considerably longer than broad, and the petioles are distinct, as in other *freycinetianum* group plants from O'ahu, Moloka'i, lowland Maui, and Kaua'i.

The measurements of the type specimen, which has broad, orbicular leaves, are the largest of any plants examined from Lāna'i and are described by Rock as the largest of any Hawaiian *Santalum*. Within certain populations there may be plants that are peculiar and represent the extremes of morphological variation. When types are based

on these peculiar specimens, other plants from the same population may not fit the basic typological concept of that taxon. *Santalum lanaiense* (Rock) seems to be based on one of these extremes, and most plants from that island do not resemble the type. Examination of other specimens from Lāna'i showed that the leaf length is often twice the width, with one of the examined specimens (*Deg., Deg. & Desha* 24,257) having leaves 2.5 times longer than wide. In the specimens with such elliptic leaves, the petioles are distinct.

Many of the specimens from Lāna'i are similar to some plants of *Santalum freycinetianum* var. *auwahiense* and to plants intermediate between *S. freycinetianum* var. *auwahiense* and *S. haleakalae*. *Santalum freycinetianum* var. *lanaiense* may be distinguished from those other taxa on the basis of the dark-green leaves and the conspicuous venation on the lower surface of the leaf.

4. ***Santalum freycinetianum* Gaud. var. *pyrularium* (Gray)** comb. nov.
   S. pyrularium Gray 1860, Diagnosis of the species of sandalwood (*Santalum*) of the Sandwich Islands, Proc. Amer. Acad. Arts 4:326–327. Type: USEE (K), Kaua'i, Sandwich Islands; Gray (ms), Mann (1866), Wawra (1875), Hillebrand (1888), Rock (1913, 1916), Skottsberg (1926, 1927), Degener (1940*a*), Skottsberg (1944), Degener and Degener (1956), St. John (1973).
   S. freycinetianum Gaud. var. *ellipticum* Hillebrand 1888 (*pro parte*).
   S. pyrularium Gray var. *sphaerolithos* Skottsberg 1944; Degener and Degener (1956), St. John (1973).
   S. freycinetianum Gaud. Stauffer 1964, annotations in herbaria (BISH, HAW).
   S. ellipticum (*auct. non* Gaud.) Sinclair 1885; Heller (1897), Rock (1916).

This taxon has been recognized in the past as the only species of the *freycinetianum* group that occurs on Kaua'i. It is usually found in middle-to-high elevations on that island. Previous descriptions are generally accurate (Rock 1913, 1916, Degener and Degener 1956), but the taxon here is recognized to encompass a greater range of variation than has heretofore been reported. Some collections had flowers 7 mm long including the tube, lobes, and pedicel. This is shorter than the recorded measurements for the flowers of this taxon and falls into the range of flower length for *S. freycinetianum*. Another characteristic that has been used to separate *S. pyrularium* from *S. freycinetianum* is the rugose nature of the endocarp; this has also been seen to be inconsistent in some plants of *Santalum* from Kaua'i (Skottsberg 1944).

Since these two characters have been shown to be variable in plants from Kaua'i, it would seem that *Santalum pyrularium* should be united with *S. freycinetianum*, as Skottsberg (1944) suggested might be necessary. The combination of *S. freycinetianum* var. *pyrularium* comb. nov. is therefore proposed.

Stauffer's herbarium annotations (1964), seem to indicate that he intended to include *Santalum pyrularium* in *S. freycinetianum*, but there is no indication that he would have recognized that taxa even varietally distinct. Considering the differences between the taxa, it seems warranted to retain *pyrularium*, at least at the varietal level. The most commonly seen plants of *Santalum* in the *freycinetianum* group from the island of Kaua'i are clearly distinct from *S. freycinetianum* var. *freycinetianum* based on the extremely long flower and drupe length, but inasmuch as the two taxa are obviously closely related, and some specimens from Kaua'i are barely distinguished from O'ahu plants, the Kaua'i plants are recognized here at the varietal, rather than specific rank.

5. *Santalum haleakalae* Hillebrand 1888, Flora of the Hawaiian Islands Heidelberg. Type: Hillebrand (B), Haleakalā 8000–10,000 ft; Rock (1913, 1916), Skottsberg (1926, 1927), Degener (1940*a*, 1940*b*), Stauffer [1964, annotations in herbaria (BISH, HAW)], St. John (1973).

S. pyrularium Gray var. β, Gray (ms); Mann (1866).
S. freycinetianum Gaud. var. *latifolium* Wawra 1875.

Typical *Santalum haleakalae* Hbd. are distinctive small trees that can be found up to tree line on the slopes of Haleakalā on east Maui, and within the crater proper. This taxon has been adequately described (Hillebrand 1888, Rock 1913, 1916, Degener 1940*a*, 1940*b*), and as it is presented here is strictly a high-elevation species with its own characteristic gross and minute morphology. It is distinguished from *S. freycinetianum* var. *auwahiense* by its smaller, often purplish green leaves and its congested bracteate inflorescence. The peculiar bottle-shaped adaxial foliar epidermal cells discovered in microscopic studies are restricted to this taxon (Stemmermann 1980).

Summary of the freycinetianum group

When all the red-flowered sandalwoods are considered, the distinction between taxa is often not clear-cut. Some red-flowered sandalwoods from Moloka'i are quite similar to *Santalum freycinetianum* from O'ahu. There are also specimens on Moloka'i that most closely resemble those from middle elevations on Maui. On Maui there is a definite intergradation between the lowland plants, now referred to as *S. freycinetianum* var. *auwahiense*, and typical alpine to subalpine *S. haleakalae*. The plants from Lāna'i are not unlike many of the variable forms of the intergrading population between *S. freycinetianum* var. *auwahiense* and *S. haleakalae*.

At one time the islands of Maui, Lāna'i, and Moloka'i were not separated (Macdonald and Abbott 1970) as they are today; they formed the landmass Maui Nui. The lowland and middle-elevation Maui Nui plants are variable, and previously a single variable taxon may have existed on all three islands. Isolation of groups of characters occurred when eustatic changes in the ocean level caused the separation of Maui Nui into separate islands. For the most part the habitat of the lowland taxa has been destroyed, and conclusions on relationships between populations on these islands must be drawn from the remaining fragmentary evidence. In addition to habitat destruction, the lowland trees would have been the first harvested for the sandalwood trade because of their accessibility, and the effects of that trade cannot be fully known. If the Maui Nui plants are to be considered to belong to a single taxon, then *Santalum haleakalae* has priority. This was apparently Stauffer's opinion, though he did not know of the Moloka'i plants. If a single taxon distinct from *S. haleakalae* is to be recognized, the epithet *lanaiense* has priority at both specific and varietal rank.

I have chosen to recognize separate taxa at the varietal rank from each of the now extant islands of Maui Nui, but I also recognize that they are closely related.

Ellipticum group

6. *Santalum ellipticum* Gaudichaud 1830, Voyage autour du monde ..., Botanique, p. 442. Type: Gaudichaud (P), Wahou (with *S. freycinetianum*); Skottsberg (1926, 1927), Degener (1937*a*), Egler (1939), Degener (1940*a*), Fosberg (1962), Stauffer [1964, annotations in herbaria (BISH, HAW)], St. John (1973).
   S. album L. var. *ellipticum* Meurisse 1892.
   S. cuneatum (Hbd.) Rock 1916; Skottsberg (1926, 1927).
   S. cuneatum (Hbd.) Rock f. *gracilius* (nomen nudum) Skottsberg 1926.
   S. cuneatum (Hbd.) Rock var. *gracilius* Skottsberg 1927.
   S. ellipticum Gaud. var. *gracilius* (Skottsberg) Degener 1937*a*.
   S. freycinetianum (*auct. non* Gaud.) Gray ms; Hillebrand (1888).
   S. freycinetianum (*auct. non* Gaud.) var. *gaudichaudii* (nomen nudum) Gray ms; Mann (1866).
   S. freycinetianum (*auct. non* Gaud.) var. *cuneatum* Hillebrand 1888.

This study has helped delimit the distribution of *Santalum ellipticum* Gaud. [as presently circumscribed to include *S. cuneatum*

(Hbd.) Rock as recommended by Egler (1939)]. *Santalum ellipticum* Gaud. is a very variable taxon; it includes plants that are generally shrubs, to trees rarely exceeding 5 m in height, with variable leaf morphology. The leaves may be sessile or petiolate, orbicular to narrowly elliptic, and semisucculent to almost chartaceous. The upper and lower surfaces of the leaves are the same gray-green color. Several subspecific taxa of *S. ellipticum* have been named, but they are merely extreme members of this variable taxon. Of the subspecific taxa that have been proposed, I recognize only *S. ellipticum* var. *littorale* (discussed later).

Earlier authors considered *Santalum ellipticum* to exist on all the major islands, including Kaho'olawe (Skottsberg 1927, Stearns 1940, Lamoureux 1970), except Kaua'i, with only a very few specimens having been cited from the island of Hawai'i. The present study has established its presence on both these islands. That *S. ellipticum* has not been recognized in the past from the island of Kaua'i is difficult to explain, and can only be attributed to the lack of collections from dry to mesic areas of Kaua'i. It appears that such areas have been neglected by past collectors, as in recent years several interesting finds have been made there. Though St. John (1973) includes *S. ellipticum* from Kaua'i in his checklist, it seems appropriate to cite the following collections, since earlier authors have excluded it: BISH: *J. Fay* 147, Hā'ele'ele Ridge; *G. Spence* 184, Jeep road to Waimea Canyon, junction with Huluhuluwai Ridge; *D. Herbst* 2106, Waimea Canyon Rd., 5 mi above Waimea; *D. Herbst* 2043, Waimea Canyon Rd., 5 mi above Waimea. HAW: *L. W. Bishop & D. Herbst* 1298, bluff above Koai'e Stream; *S. Montgomery* s.n. Koai'e Canyon; *L. Stemmermann & L. Gilbert* 781, Waimea Canyon Rd.

For the most part, collections from the island of Hawai'i are better referred to *Santalum paniculatum* than to *S. ellipticum*. In his consideration of the genus *Santalum*, Skottsberg (1927) recognized *S. ellipticum* only from the island of O'ahu, but he considered *S. cuneatum* to occur on all the islands except Kaua'i. He cited numerous specimens for each island, but only a single one was cited from Hawai'i, though later Skottsberg (1944) cited another. Similarly, Egler (1939) recognized *S. ellipticum* from all islands except Kaua'i, and like Skottsberg, he cited several specimens from each of the other islands but listed only one from Hawai'i. Degener (1937*a*) stated that *S. ellipticum* "probably" could be found on Hawai'i, so he too has felt reservations concerning its occurrence there. Though apparently not convinced of the occurrence of *S. ellipticum* on Hawai'i, he has described two forms of *S. ellipticum* from Hawai'i and transferred *S. pilgeri* var. *luteum* to *S. ellipticum*.

Studies of foliar anatomy of the Hawaiian species of *Santalum* have demonstrated that *S. ellipticum* can be distinguished from *S. paniculatum* and *S. paniculatum* var. *pilgeri* by the presence of stomata on the adaxial epidermis (Stemmermann 1980). Use of this characteristic to define the taxon enables me to confirm the presence of *S. ellipticum* on Hawai'i. There seems to be only a single known population, which now exists in disjunct pockets in the gulches of predominantly exotic pastureland on the leeward side of the Kohala Mountains, but other populations may also exist. From the paucity of material of *S. ellipticum* from the island of Hawai'i deposited in local herbaria, and from my own observations in the field, I conclude that *S. ellipticum* is not at all common on the island of Hawai'i. Specimens of this taxon that have been examined from the island of Hawai'i are: BISH: *Ewart* 345, 1800 ft elev. on the Kawaihae Rd. (I was unable to locate *Neal* 345 from Hawai'i, cited by Egler—presumably this was Ewart's collection which has been identified by Neal); *E. Hosaka* 2047, South Kohala, Waimea Range Paddock, 1800 ft. HAW: *L. Stemmermann & W. Gagné* 794, Kohala pastureland, 3000 ft.

7. *Santalum ellipticum* Gaud. var. *littorale* (Hbd.) Skottsberg

   S. freycinetianum (*auct. non* Gaud.) var. *littorale* Hillebrand 1888, Flora

of the Hawaiian Islands, Heidelberg. Type: Hillebrand (B), O'ahu, Cape Kaena, and Kailua near seashore [no type stated by Hillebrand, but Skottsberg (1927) lists the Kaena specimen based on location data given in the label of the type].

S. littorale Rock 1916.

S. cuneatum (Hbd.) Rock var. *laysanicum* Rock 1916; Skottsberg (1927).

S. ellipticum Gaud. var. *littorale* (Hbd.) Skottsberg 1927; Fosberg (1962), St. John (1973).

S. ellipticum Gaud. f. *physophora* Degener 1937*a*.

S. ellipticum Gaud. *sensu* Egler 1939 *pro parte*; *sensu* Stauffer [1964, in herbaria (BISH, HAW)].

S. freycinetianum (*auct. non* Gaud.) Bitter 1900.

This taxon can be distinguished from *Santalum ellipticum* var. *ellipticum* by its very succulent leaves and low stature. Though it is presently known only from O'ahu, it was once on Laysan Island, but browsing by feral rabbits has caused its extinction there (Christopherson and Caum 1931, Lamoureux 1963, Ely and Clapp 1973). There may also be coastal populations of this taxon that have not been recorded on some of the other main islands.

Intergradation is evident between *Santalum ellipticum* var. *littorale* and var. *ellipticum*. The coastal populations of *S. ellipticum* var. *littorale* have thick orbicular leaves, and short petioles, as well as very glaucous fruit. Plants growing inland belonging to *S. ellipticum* var. *ellipticum* have thinner elliptic leaves with longer petioles. Presumably, these variations are under both genetic and ecological influence. Authors have chosen to recognize such variation in different ways and have based varieties (Hillebrand 1888, Skottsberg 1927, St. John 1973), forms (Degener 1937*a*), and even species (Rock 1916), on such differences. Egler (1939) simply recognized the species as being quite variable without recognizing any subspecific taxa. In my opinion there are sufficient differences (succulence, subsessile leaves, glaucousness of the fruit, and low stature) in this group to recognize the coastal populations as distinct at the varietal rank. They should therefore be recognized as *S. ellipticum* var. *littorale* (Hbd.) Skottsberg.

8. *Santalum paniculatum* Hooker & Arnott 1932, The botany of Captain Beechey's voyage, London. Type: Macrae (K), from the "volcano of Owhyee"; Rock (1913, 1916), Skottsberg (1926, 1927), Degener (1930, 1940*a*), Stauffer [1964, in herbaria (BISH, HAW)], St. John (1973).

S. pilgeri Rock var. *luteum* Rock 1916; Skottsberg (1927).

S. ellipticum Gaud. var. *luteum* Degener 1937*a pro parte*; Fosberg (1962).

S. ellipticum Gaud. f. *annectens* Degener 1937*a*; St. John (1973).

S. paniculatum H. & A. var. *chartaceum* Degener and Degener 1973.

S. ellipticum Gaud. var. *latifolium* (Gray) Fosberg 1962; St. John (1973).

The other two taxa on Hawai'i are both also in the *ellipticum* group. *Santalum paniculatum* H. & A., which is restricted to Hawai'i, includes shrubs and trees from many areas of the island. The type collected from near Kīlauea volcano (Macrae 1922) represents typical *S. paniculatum*. It can be distinguished from the closely related *S. paniculatum* var. *pilgeri* (with which it intergrades) by the papillate character of the lower epidermis, which causes the lower leaf surface of *S. paniculatum* to appear pale, or sometimes rusty yellow. Fosberg (1962) has provided the appropriate combination (*S. ellipticum* var. *latifolium*) for recognizing *S. paniculatum* as a variety of *S. ellipticum*, and Degener (1937*a*) apparently recognizes plants intermediate between *S. paniculatum* and *S. pilgeri* as varieties of *S. ellipticum*. However, my studies have shown that *S. ellipticum* should be considered distinct from these other two taxa of the *ellipticum* group because of the presence of stomata on the upper leaf surface in *S. ellipticum*.

The leaves of *S. paniculatum* are coriaceous, subsessile to petiolate, and are often yellowish orange, especially in exposed areas where there is little to no shade. Plants

grown in the shade have chartaceous leaves of a bluish hue. The difference in coloration is due to the accumulation of substances (presumably tannins) in the leaves of the exposed plants.

9. ***Santalum paniculatum* Hook. & Arn. var. *pilgeri* (Rock)** comb. nov.
   - *S. pilgeri* Rock 1916, The sandalwoods of Hawaii, Hawaiian Bd. Agr. For. Bot. Bull. 3. Type: *Rock* 10,033 (BISH), Pulehua above Kealakekua, north Kona, elev. 5000 ft; Skottsberg (1927), Degener (1940*a*).
   - *S. ellipticum* Gaud. var. *luteum* Fosberg 1962 *pro parte*; St. John (1973).
   - *S. paniculatum* Hook. & Arn. *sensu* Stauffer *pro parte*, in herbaria (BISH, HAW).
   - *S. freycinetianum* (*auct. non* Gaud.) Hillebrand 1888 *pro parte*; Rock (1913).
   - *S. freycinetianum* (*auct. non* Gaud.) var. *latifolium* Hillebrand 1888 *pro parte*.

Typical *Santalum pilgeri* Rock is found in north and south Kona on Hawai'i. Plants of this taxon are trees, to 65 ft high (L. W. Bryan 1974), with chartaceous olive-green leaves. The lower surfaces of the leaves of this taxon are dull, but not considerably paler than the upper surface, as are the lower surfaces of the leaves of *S. paniculatum*. Another characteristic of this taxon is that its leaves are often convex and chewed by insects. Though typical *S. pilgeri* from above Kealakekua, north Kona, and *S. paniculatum* from Kīlauea are clearly distinguishable, the intergradation is considerable and clear-cut differences are absent.

Apparently, in his visit to Hawai'i in 1964, Stauffer never saw typical *Santalum pilgeri* from Kealakekua Ranch, and he annotated specimens of that taxon as *S. paniculatum*. I feel that the taxon should be recognized as varietally distinct, and as the specific epithet *paniculatum* has priority over *pilgeri*, the correct name for that taxon is *S. paniculatum* var. *pilgeri* (Rock) comb. nov.

While Fosberg (1962) suggests that the epithet *luteum* has priority in the varietal rank for *Santalum pilgeri*, I disagree. Having examined the type for *S. pilgeri* (*Rock* 10,033 BISH) and populations in the type locality (Pulehua above Kealakekua), as well as the type for *S. pilgeri* var. *luteum* (*Rock* 12,515 BISH) and plants in the type locality (Hualālai), I conclude that the plants from Hualālai are one of the myriad of forms transitional between typical *S. paniculatum* and *S. pilgeri sensu stricto*. Therefore, at the varietal rank, the proper combination is that given above, and *S. pilgeri* var. *luteum* is considered here within the circumscription of *S. paniculatum*.

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